The origin of the mammalian fauna of Sulawesi (Celebes)

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It has long been appreciated that within the Indonesian archipelago lies one of the most remarkable zoogeographical boundaries in the world. In Java, Sumatra and Borneo may be found the typical Oriental Fauna, with representatives of the Pongidae, Cercopithecidae, Lorisidae, Felidae, Mustelidae, Elephantidae, and other families from many mammalian orders; in New Guinea, 1300 km due east, none of these groups occur, indeed no placental order appears to be indigenous except the Rodentia, and the most conspicuous mammals, the Marsupials, are absent from the Oriental region.

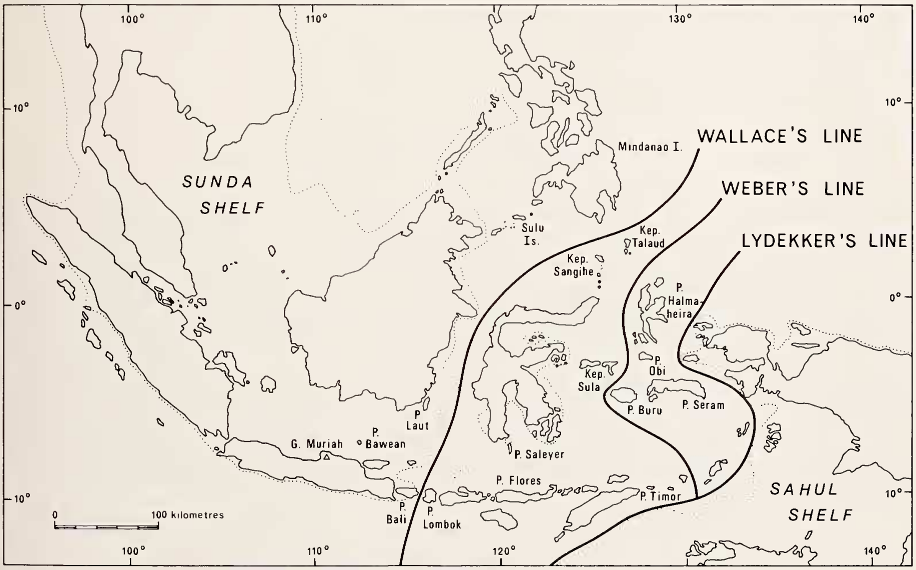

Fig. 1. Map of the Indo-Australian Archipelago showing the three faunal lines — Wallace's, Weber's and Lydekker's — discussed in the text of this paper

But this is not the whole story. The bulk of the Oriental fauna is already missing from Sulawesi, only 50 km from Borneo across the Makassar straits; and the islands closest to New Guinea, such as Seram and Halmaheira, already lack the major part of the latter's fauna. To the south, Lombok appeared to some authors to be gravely depauperate compared to Bali; Timor, compared to Australia. Two standard text-books of zoogeography represent this situation in slightly different ways: de Beaufort (1951) treats it in terms of three faunal lines – Wallace's, Weber's and Lydekker's – while Darlington (1957) prefers to qualify the zone itself as a "Subtraction-transition zone".

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The first of the three lines to be drawn was Wallace's line; de Beaufort gives some of the history of the controversies over this line. Much of the controversy has been concerned solely with whether the line is worth recognising, and if so whether the Philippines belong to the west or east of it; no author has disputed the fact that there is a striking change between Borneo and Sulawesi, but few have really asked themselves what this change means. This has resulted in Wallace's line acquiring a nearly magical significance, as — in its worst manifestation — a sharp boundary between two different faunal universes. The fact that Lydekker's line, to the east, marks as sharp a delimitation as does Wallace's line to the west, is a contribution made by de Beaufort himself; only *Phalanger, Melomys* and *Rattus ruber* cross it to reach Halmaheira, and these plus a distinctive Peramelid and a specialised *Rattus*-like form reach Seram. The difference between the two is that the islands to the west of Lydekker's line are simply depauperate: they cannot, with the possible exception of Seram, be said to have a fauna of their own as far as mammals are concerned, whereas Sulawesi, to the east of Wallace's line, does have a distinct and characteristic fauna of its own.

This, of course, applies to the northern part of the region in question; in the southern part, along the Lesser Sunda islands (Nusatenggara), both Timor and Flores have an endemic fauna, which will be the subject of a later paper, and the differences between Bali and Lombok are less marked than those between Borneo and Sulawesi. But in the present paper only Sulawesi will be discussed.

The geographical situation

Java, Sumatra and Borneo lie on the Sunda shelf, with a maximum depth of sea between them of some 60 metres. During a period of glaciation in the temperate zones therefore, when the sea level fell world-wide by much more than this, these three islands would have been joined to each other and to the mainland of south-eastern Asia. (That they were drained by several very broad and long rivers, and were anything but a uniform land mass, has escaped the attention of biogeographers until very recently.) However the depth of the Makassar Strait is much more than this, and barring tectonic activity Sulawesi would never have been connected to Sundaland. This explains why the fauna of Sulawesi is different; it is the task of the present paper to examine just how it is different, and when and how it was populated with mammals.

The present mammal fauna of Sulawesi

The present fauna of Sulawesi as far as mammals are concerned is listed in Table 1, which is divided into eight subsections: Endemic genera, Endemic subgenera, Endemic species of more widespread genera, Species extending to the Moluccas only, Species extending to the Australian region, Species extending to Sundaland, Species extending to the Philippines, and Species of wide distribution. Some species fall into more than one category.

1. Endemic genera. These are 13 in number: 12 living, one known only as a fossil. Three are bats, one a carnivore, two (including the fossil) are suid artiodactyls, and seven are rodents (two sciurids, five murids). Strictly speaking, *Babyrousa* occupies a special position, as it is not restricted to Sulawesi but occurs also on the Sula islands and Buru; it might therefore better have been placed in group 4, but it is the only species of its genus and has doubtless originated on Sulawesi.

2. Endemic subgenera. Only a formality of taconomy separates this group from the first. *Cynopithecus* is here given subgeneric rank, contrary to FOODEN (1969), only for ease of reference: they are certainly derived from a single invasion of Sulawesi, although there may indeed be seven species as FOODEN suggests.

It is worth noting that all these genera and subgenera, with two exceptions, are monotypic. Mostly they are forms of restricted distribution, generally found only on high mountains, with less distinctive relatives on the island which have evidently out-competed them on the lowlands. But both monkeys *(Macaca)* and buffaloes *(Bubalus)* are the only representatives of their families on the island, and have speciated in the absence of competition.

3. Endemic species in widespread genera. This group certainly represents a different level of distinctness from the last two, and so almost certainly a later invasion: with the exception of the two fossil Proboscideans, in whose case we are of course looking at a different time segment. Some of the *Rattus* species-groups (see below) may equally represent an earlier invasion.
4. As was stated above, the Moluccas (Moluku) have no endemics of their own, above the subspecific level; with the exception of the dubious genera *Rhynchomeles* and *Nesoromys* on Seram, and a few bats and rodents which (J. E. HILL, in litt.) seem to be slightly differentiated representatives of New Guinea or Sulawesi species. The most likely explanation of Group 4 therefore, is that these are all (mostly?) migrants from Sulawesi.
5. The species whose ranges extend to New Guinea and/or Australia are all bats. While the theoretical standpoint that "bats fly so can get from island to island" does not hold in all cases — instance the occurrence of the Sulawesi endemic bats — the widespread bats of this and succeeding groups are indeed wide-ranging forms which would be easily dispersed by wind, or perhaps by choice.
6. The bats of Group 6, whose range extends to Sundaland, are wide-ranging forms like those of Group 5. The porcupine, the civet and the deer are almost certainly introduced (see below); the pig needs further study (also see below).
7. Only five species of mammal, except for group 8, are in common between Sulawesi and the Philippines; all are bats, and three of them belong also to groups 5 or 6.
8. In this group are included species whose range extends all three ways from Sulawesi: west to Sundaland, north to the Philippines and east to New Guinea. They are quite certainly introduced to Sulawesi; and, with the possible exception of *Rattus exulans,* surely introduced from Sundaland. As staded above, the Group 6 species are also introduced from Sundaland, but they happen not to have got much farther east (except to some of the Moluccas).

Relationships of Sulawesi mammals

The figures of relationships extracted from Table 1 are presented in Table 2. Conveniently, 100 species at present inhabit Sulawesi: this excludes Group 8. 40 % of the genera and subgenera represented on the island are endemic to it. 71 % of the species are endemic: an extraordinarily high figure, and if one grants that group 4 species are probably derived from Sulawesi and includes them in the total of endemics, the figure rises to 80 %. Whatever else one believes about the Sulawesi mammals, it becomes clear that in geologically recent times it has been extraordinarily difficult for them to get on or off it.

It has been suggested to me (P. J. H. VAN BREE, in litt.) that including the bats could seriously prejudice the results in a number of ways. Not only, as remarked

Table 1

Mammalian fauna of Sulawesi (Celebes)

			Number of Species
1. Endemic genera			
CHIROPTERA	Pteropodidae	*Boneia* Jentink, 1879	1
		Neopteryx Hayman, 1946	1
		Styloctenium Matschie, 1899	1
CARNIVORA	Viverridae	*Macrogalidia* Schwarz, 1910	1
ARTIODACTYLA	Suidae	*Babyrousa* Perry, 1811	1
		† *Celebochoerus* Hooijer, 1954	1
RODENTIA	Sciuridae	*Prosciurillus* Ellerman, 1947	1
		Hyosciurus Archbold & Tate, 1935	1
	Muridae	*Lenomys* Thomas, 1898	1
		Eropeplus Miller & Hollister, 1921	1
		Echiothrix Gray, 1867	1
		Melasmothrix Miller & Hollister, 1921	1
		Tateomys Musser, 1969	1
2. Endemic subgenera			
CHIROPTERA	Vespertilionidae	*Myotis (Chrysopteron* Jentink, 1910)	1
PRIMATES	Cercopithecidae	*Macaca (Cynopithecus* Geoffroy, 1835)	1—7
ARTIODACTYLA	Bovidae	*Bubalus (Anoa* H. Smith, 1827)	2
RODENTIA	Sciuridae	*Callosciurus* (*Rubrisciurus* Ellerman, 1954)	1

			Related species' distribution
3. Endemic species of more widespread genera/subgenera			
MARSUPIALIA	Phalangeridae	*Phalanger ursinus* (Temminck, 1824)	New Guinea
LIPOTYPHLA	Soricidae	*Crocidura elongata* Miller & Hollister, 1921	Sundaland
		4 other spp., status dubious	
CHIROPTERA	Pteropodidae	*Pteropus arquatus* Miller & Hollister, 1921	?
		Rousettus celebensis Andersen, 1907	Sundaland
		Dobsonia exoleta Andersen, 1909	New Guinea
		Eonycteris rosenbergi (Jentink, 1899)	Sundaland
	Rhinolophidae	*Rhinolophus celebensis* Andersen, 1905	Sundaland
		Hipposideros pelingensis Shamel, 1940	New Guinea
		Hipposideros inexpectatus Laurie & Hill, 1954	New Guinea
	Molossidae	*Tadarida sarasinorum* (Meyer, 1899)	Sundaland
		Cheiromeles parvidens Miller & Hollister, 1921	Sundaland
	Vespertilionidae	*Pipistrellus minahassae* (Meyer, 1899)	Sundaland
		Scotophilus celebensis Sody, 1928	Sundaland
		Kerivoula aerosa Tomes, 1858	Sundaland
		Kerivoula rapax (Miller, 1931)	New Guinea
PRIMATES	Tarsiidae	*Tarsius spectrum* (Pallas, 1779)	Sundaland
PROBOSCIDEA	Stegodontidae	† *Stegodon sompoensis* Hooijer, 1964	Sundaland
	Elephantidae	† *Elephas celebensis* (Hooijer, 1949)	Sundaland
RODENTIA	Sciuridae	*Callosciurus* 4 spp., status dubious	Sundaland
	Muridae	*Haeromys minahassae* (Thomas, 1896)	Sundaland
		Rattus 24 spp.	Various

Table 1 (continued)

4. Species extending to Moluccas only		
MARSUPIALIA	Phalangeridae	*Phalanger celebensis* (Gray, 1858)
CHIROPTERA	Pteropodidae	*Pteropus griseus* (Geoffroy, 1810)
		Pteropus caniceps (Gray, 1870)
		Pteropus personatus Temminck, 1825
		Acerodon celebensis (Peters, 1867)
		Thoopterus nigrescens (Gray, 1870)
		Nyctimene minuta Andersen, 1910
	Vespertilionidae	*Pipistrellus petersi* (Meyer, 1899)
5. Species extending to New Guinea/Australia		
CHIROPTERA	Pteropodidae	*Pteropus hypomelanus* Temminck, 1853
		Pteropus alecto Temminck, 1837
		Macroglossus lagochilus Matschie, 1899
		Nyctimene cephalotes (Pallas, 1767)
	Rhinolophidae	*Hipposideros cervinus* (Gould, 1863)
		Hipposideros diadema (Geoffroy, 1813)
	Vespertilionidae	*Pipistrellus papuanus* (Peters & Doria, 1881)
		Myotis adversus (Horsfield, 1824)
6. Species extending to Sundaland		
CHIROPTERA	Pteropodidae	*Cynopterus brachyotis* (Müller, 1838)
		Macroglossus lagochilus Matschie, 1899
	Emballonuridae	*Emballonura monticola* Temminck, 1838
	Megadermatidae	*Megaderma spasma* (Linnaeus, 1758)
	Vespertilionidae	*Pipistrellus javanicus* (Gray, 1832)
		Pipistrellus imbricatus (Horsfield, 1824)
		Myotis adversus (Horsfield, 1824)
		Tylonycteris robustula Thomas, 1915
		Kerivoula hardwickei (Horsfield, 1824)
CARNIVORA	Viverridae	*Viverra tangalunga* Gray, 1832
PROBOSCIDEA	Stegodonidae	† *Stegodon trigonocephalus* Martin, 1887
ARTIODACTYLA	Suidae	*Sus verrucosus* Müller & Schlegel, 1845
	Cervidae	*Cervus timorensis* de Blainville, 1822
RODENTIA	Hystricidae	*Hystrix javanica* (F. Cuvier, 1823)
	Sciuridae	*Callosciurus prevostii* (Desmarest, 1822)
		Callosciurus notatus (Boddaert, 1785)
7. Species extending to the Philippines		
CHIROPTERA	Pteropodidae	*Cynopterus brachyotis* (Müller, 1838)
	Emballonuridae	*Emballonura alecto* (Eydoux & Gervais, 1836)
	Megadermatidae	*Megaderma spasma* (Linnaeus, 1758)
	Rhinolophidae	*Rhinolophus philippinensis* Waterhouse, 1843
	Vespertilionidae	*Tylonycteris robustula* Thomas, 1915
ARTIODACTYLA	Suidae	*Sus verrucosus* Müller & Schlegel, 1845
8. Species of wide distribution (includes Sundaland, Philippines, Moluccas etc.)		
CARNIVORA	Viverridae	*Paradoxurus hermaphroditus* (Pallas, 1777)
RODENTIA	Muridae	*Rattus rattus* (Linnaeus, 1758)
		Rattus argentiventer (Robinson & Kloss, 1916)
		Rattus exulans (Peale, 1848)
		Rattus norvegicus (Berkenhout, 1769)
		Rattus nitidus (Hodgson, 1845)
		Mus musculus Linnaeus, 1758

Table 2

Relationships of mammals of Sulawesi

	Number	Percent	Excluding Chiroptera Number	Excluding Chiroptera Percent
Total number of living species	100		59	
Endemic genera (living)	13	29	10	55
Endemic genera and subgenera	17	40	13	58
Endemic species		71	54	92
Species shared only with Moluccas		9	2	4
Total, endemic plus semi-endemic species		80	56	95
Species shared with Moluccas and with —				
New Guinea		8	0	0
Sundaland		66	1	2
Total shared with Moluccas		22	3	6
Species shared with New Guinea but not with Moluccas		2 (incomplete data?)	0	0
Species shared with Sundaland		15	3	3
Species shared with the Philippines		5	1	2
Among the endemic/semi-endemic species of widespread genera (excluding *Rattus*) — Belong to western (Sundaland) groups	29	68	21	91
Belong to eastern (New-Guinea/Australia) groups	6	14	2	9

The species of Table 1, Group 8 (widespread distribution) are not included in the total of this table.

above, do some bats occur very widely and have a remarkable facility for dispersal, but equally their occurrence, distribution and taxonomy are very poorly known: considerably less well-known, for example, than in the case of the Rodentia. When it is realised that nearly half (41 out of 100) of the mammal species of Sulawesi belong to the Chiroptera, the validity of this argument becomes apparent. Therefore in Table 2 comparative data are represented for the total mammal fauna and for the true "land mammals" (i. e. without the bats).

Now the total of endemic genera plus subgenera rises to nearly 60 %, and over ninety percent of the species are endemic. The evident isolation of the island stressed previously is fully endorsed: of those species that have managed to get on or off it, all but three are flying mammals.

Eight species, all bats, extend to New Guinea via the Moluccas, and two *(Pteropus alecto, Myotis adversus)* extend to New Guinea but are not so far known from the Moluccas. This makes 10 altogether which are in common with New Guinea, compared to 15 with Sundaland, 5 with the Philippines; excluding the bats, no species are in common with New Guinea, three with Sundaland, one with the Philippines. This makes sense if, as seems plausible, these are the result of waif dispersal: Sulawesi is across a narrow strait from Sundaland but rather far from both New Guinea and the Philippines. Of the endemic species whose relationships can be easily traced (and here the poorly known unwieldy genus *Rattus* is excluded), 68 % total (91 % excluding bats) belong to western groups, only 14 % (9 % excluding bats) to eastern; adding these to the respective figures of actual species in common, we can say that 80 % of Sulawesi species (94 % excluding bats) have detectable western affinities, 18 % (9 % without bats) have detectable eastern affinities, 5 % (2 % without bats) have Philippine affinities. These totals, however, are not mutually exclusive.

Various authors, especially HOOIJER (1958) and DE BEAUFORT (1951), have postulated a Philippine origin for a large part of the Sulawesi fauna. It has been seen above that as far as the mammals are concerned this is quite out of the question. The Anoa *(Bubalus [Anoa]* spp.) is said by DE BEAUFORT to be related to the Tamarau, another dwarf buffalo, from Mindoro in the Philippines, but the two are definitely independent dwarfings (GROVES 1969). Recently NIEMITZ (1974) has invoked a dispersal the other way, to the Philippines, for *Tarsius,* but this again is susceptible of a more likely alternative explanation. DOBRORUKA (1971) finds *Cervus timorensis* in the Philippines, but no securely localised specimen has come from there (GRUBB and GROVES, in preparation).

Examples of some relationships are discussed below:

Phalanger: Two species occur on Sulawesi: the only marsupials which occur so far west. TATE (1945) places *P. celebensis* in the *orientalis* group as a distinct species whose range includes Taliabu I. (Sula group) and Great Obi (Moluku), *P. orientalis* being found on the other Sula and Molucca islands. To judge from TATE's descriptions there would be in fact no sharp distinction between the two, it being merely a matter of typology whether one draws the line on the basis of mastoid form, incisor-canine diastema, or colour. There is really a graded series, with the Obi, Taliabu and Peleng races of *celebensis* intermediate.

P. ursinus is more distinct, and TATE (loc. cit.) puts it in a species-group by itself, but notes that it may be distantly related to *P. maculatus;* it is restricted to Sulawesi and the Talaud islands, but on Saleyer island *P. maculatus* occurs, in a race *(chrysorrhous)* evidently indistinguishable from that of most of the Moluccas, and showing some resemblance in pelage to the Talaud race of *P. ursinus.*

Obviously the genus needs revision to determine the distinctness of the various allopatric species and the significance of the curious interdigitation of their ranges. Both species occur on Toalian sites on the southwestern peninsula of Sulawesi (HOOIJER 1950); that is to say, probably early Holocene, but prior to the arrival of domesticates such as dog and pig, or of definite introductions such as deer.

Cuscus are carried around by man as food sources; they appear to have arrived in Timor subsequent to 500 B.C. (GLOVER 1970) along with pig and deer, and it is possible that *P. celebensis* might be so introduced, although unlikely, and certainly not at all likely in the case of *P. ursinus.* Cuscus seem to be highly adaptable animals, like the closely related *Trichosurus* of Australia, and waif dispersal would be relatively easy.

Tarsius: NIEMITZ (1974) in a painstaking study has elucidated the relationships of the three species of *Tarsius.* The Sulawesi species, *T. spectrum,* is more primitive than the other two, *T. bancanus* from Sundaland (not Java) and *T. syrichta* from the southern Philippines. He favours the hypothesis, however, that the latter two are convergent in their specialisations, and independently derived from Sulawesi; this primarily because *T. bancanus* is still more highly evolved than *T. syrichta* and could not have given rise to it, also because tarsiers are not known from the Sulu islands, the route by which they would have had to have invaded the Philippines from Borneo.

Seeing the degree of convergence which would be involved, it is surely simpler to recognise that *T. bancanus* could easily have gone on evolving after the derivation of *T. syrichta* from it; and the Sulu islands fauna is extremely poorly known.

An important point however is the possibility of tarsiers having arisen in Sulawesi, and later dispersed out of it. The incomplete distribution of tarsiers in Sundaland (absent from Java and Malaya, and apparently unrecorded from much of Sumatra) and the Philippines might support the view that they are quite recent immigrants into those regions.

Macaca: The seven putative species of macaque on Celebes (FOODEN 1969) are obviously all derived from a single invasion. FOODEN suggests that they are related to *M. nemestrina,* which occurs on Borneo and is not known, even as a fossil (HOOIJER 1962) from Java; they will have entered Sulawesi, then not one island but an archipelago, from Borneo in the Pleistocene and diverged into seven species on their separate islands from the most primitive species, *M. tonkeana,* which inhabits the central portion of the present island, nearest to Borneo.

If the Sulawesi macques are to be related to any other living groups it is probably *M. nemestrina* to which they are closest; however a genus-wide survey of skulls and other features would be desirable before this affinity is considered established. According to M. H. MACROBERTS (pers. comm.) there are many differences in behaviour; within the troop, *M. nemestrina* is a non-contact species while within a troop of *M. nigra* MACROBERTS found a statistically significant tendency for clumping, with a tendency for groups already formed, their members being in bodily contact, to attract other individuals. *M. nigra* would seem in this respect to resemble the Indian *M. radiata* (ROSENBLUM et al. 1964).

SIMONS (1971) found that certain fossil monkeys from Europe, India and China resemble the "Celebes black ape" (i. e. *M. nigra*) in such features as the long face; but this could, in his view, be an artefact of large size.

Macrogalidia (see fig. 2): This endemic genus belongs to the subfamily Paradoxurinae, of which no fossil representatives are known except for an early Holocene southern subspecies of the living *Macrogalidia musschenbroekii* (HOOIJER 1950). Its absence outside the northern peninsula today may result from competition by the introduced *Paradoxurus;* although the latter is not known as a fossil on Sulawesi, it may be significant that *Macrogalidia* remains do not occur in the caves north of Cani (Tjani), the most recent deposits, where domestic animals and deer occur.

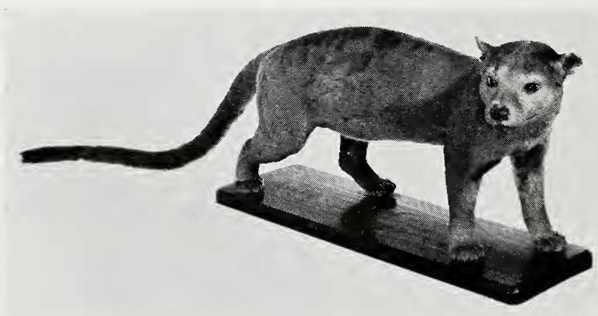

Fig. 2. Mounted male specimen of *Macrogalidia musschenbroikii* (Schlegel, 1879) from the collections of the Zoological Museum, Amsterdam. Total length about 145 cm

Macrogalidia is marginally the largest of the Viverridae: only *Arctictis* and *Cryptoprocta* closely approach it in bodily dimensions. This makes it a most remarkable exception to the "island dwarfing" rule so commonly obeyed among larger mammals. Whether this could be due to the absence of competition from other carnivores will have to await a study of its ecology: that it is carnivorous at all, rather than herbivorous or frugivorous like some other Viverrids, has never been demonstrated.

Paradoxurus hermaphroditus and *Viverra tangalunga*: These two species, the palm-civet and the Malay civet, are carried about from island to island by man: the former as a rat-catcher, the latter for its musk. Their presence on Sulawesi doubtless results from introduction in this manner.

Stegodon sompoensis: Recently HOOIJER (1974) has proposed that this is not in fact an endemic species but includes *S. timorensis* Sartono, from Timor and Flores. Stegodons from both islands are known only from teeth; while as HOOIJER shows, no difference between them can at present be sustained, the possibility remains that they may be independently dwarfed, and differences may emerge when fuller material is known. Both are derived from *S. trigonocephalus,* which is found in the Pliocene Kali Glagah beds of Java and survives at least into the Middle Pleistocene and seems also to occur in unstratified deposits in Sulawesi; a stegodon tusk fragment has been found in the still earlier (Lower Pliocene?) Ci Julang beds of Java.

Elephas celebensis: The situation here is analogous to that in *Stegodon:* MAGLIO (1973) proposed that the Sulawesi dwarf elephant, of presumably Middle Pleistocene age, is represented also on Java, in certain dental specimens some at least of which are from Middle Pleistocene Kabuh beds. In this case HOOIJER (1974) was able to find a slight difference, molars from Sulawesi being more advanced (hypsodont) than those from Java, and retained a subspecific separation. Under such circumstances, to unite the species may be premature. Both are descended (MAGLIO 1973) from *Elephas planifrons* from the Upper Siwaliks of India, known also from the Ci Julang and Kali Glagah beds of Java.

Babyrousa: THENIUS (1970) assigns this genus to a subfamily of its own; its closest relative appears to be a form from the Oligocene of Europe!

Celebochoerus: THENIUS (1970) agrees with HOOIJER (1958) that this extinct endemic genus is related not to Babyrousa but to the African bushpig, *Potamochoerus,* to which it is connected by forms from the Middle Siwaliks of India.

Sus verrucosus: The Sulawesi Warty Pig is either a distinct species (HOOIJER 1954) or a subspecies of the Javanese form (MOHR 1960). The latter author, while maintaining their conspecificity, none the less is able to point to a multiplicity of differences, such as the diminutive size of the Sulawesi race, its skull and teeth differences, differences in colouration and in the form of the warts. These are all illustrated by photographs of living animals. The skull features of the composite *Sus verrucosus* are simply (THENIUS 1970) those to be expected in primitive representatives of the genus *Sus.* It is clear that a review of South East Asia's wild pigs is in order: the present author hopes to begin a study to this end in the near future.

A further point about this species, or species-construct, is its supposed extension into the eastern Philippine islands: the only species outside the Chiroptera which is said to do so.

Sus verrucosus occurs in Java — as "*Sus macrognathus*" — as far back as the Plio-Pleistocene Pucangan beds. Pigs (the so-called *Sus stremmi* and *S. brachygnathus)* occur in the Pliocene Kali Glagah faunas; the latter has been assigned by BADOUX (1959) to a living species *Sus barbatus* which does not today occur in Java, but it must be admitted that his comparative material is very small rendering the assignment rather provisional.

Cervus timorensis: VAN BEMMEL (1949) considers this species indigenous to Sulawesi; it is not found as a fossil but, he suggests, it may have been living on other parts of the island, fossil beds being known only from the southwestern peninsula. It may be significant however that in subfossil state it appears in late deposits in the caves north of Tjani (Cani) (HOOIJER 1950), along with dogs, pigs, and domestic buffalo. This is analogous to the situation on Timor (GLOVER 1970) where deer first occur along with pottery, pigs, rats etc. after 4500 B.P. The inference that they are introduced is very strong. Deer are known to be carried around and deliberately released on islands as a meat supply.

Bubalus: The dwarf buffaloes of the subgenus *Anoa* are not related to the Philippines dwarf buffalo *(B. mindorensis)* which is on the contrary a derivative of the large Indo-Burmese buffalo *B. arnee*. The latest known fossil that could be a common ancestor of the two is *Hemibos* from the Upper Siwaliks (see Groves 1969).

Lenomys: Misonne (1969) considers this genus close to *Lenothrix* of Sundaland, but a little more advanced than the latter which is very primitive among the Muridae. Other close relatives, he suggests, may include the *Mallomys-Papagomys-Spelaeomys* group from New Guinea and Flores, and the New Guinea/Australian Pseudomyinae. *Eropeplus* is a likely relative (Misonne; Musser 1970).

Haeromys minahassae: This is related to two species which inhabit Borneo (Medway 1965). As its distribution is very limited in both islands, there is no indication whether it originated on Sulawesi and spread to Borneo, or vice versa. Misonne (1969) tentatively suggests a relationship with the Pseudomyine genus *Lorentzimys*.

Echiothrix: This is a very isolated genus; Misonne (1969) can only suggest it may be distantly related to the Hydromyinae, mostly inhabiting New Guinea but in which he also includes certain Philippine genera.

Rattus spp: Misonne (1969) recognises four subgenera of this genus; all four occur on Sulawesi. Most of the species of the subgenus *Bullimus*, the most archaic subgenus, occur on Sulawesi. As he has arranged the species, at least nine separate invasions of the island would have to have occurred, representing *(Bullimus) R. xanthurus* group, *R. dominator, R. chrysocomus* group, *R. celebensis/callitrichus* group, *(Leopoldamys) R. hellwaldi, R. whiteheadi/musschenbroeki* group, *(Stenomys) R. tatei* (synonym of *taerae* according to Musser 1971), *(Rattus) R. dammermanni, R. hoffmanni.* However, if we turn the proposition inside out and propose a Sulawesi origin for the genus as a whole, it would appear that we need postulate only four westward dispersals *(R. muelleri/everetti* group and *R. bowersi* group in *Bullimus, R. rajah/sabanus* group in *Leopoldamys, R. rattus/norvegicus* group in *Rattus),* and two eastward *(R. niobe/assimilis* group in *Stenomys, R. lutreolus* group in *Rattus).*

This is of course all very theoretical, but Misonne's view are not universally accepted. Musser (1973 and other papers) offers several alternative dispositions of species. In his 1973 paper the latter author offers an interim list of 24 species on Sulawesi, with the qualification that some may not remain in the genus at all, and some changes are bound to be made in the final list. "These species", he states, "are native to Celebes and its offshore islands, including the Sula Islands, and do not occur elsewhere. Their closest relatives are found primarily on islands of the Sunda Shelf and on the mainland of Southeast Asia; a few occur in the Philippines". He contrasts the distinctiveness of these native species, from each other and from their near relatives, with the situation in the five commensal species (listed in Table 1, group 8) which hardly differ from island to island.

Melasmothrix and Tateomys: Musser (1969) considers these genera related to each other and perhaps to the *Rattus chrysocomus* group. This is a group of very primitive *Rattus* according to Misonne (1969). Their origin will thus probably be from within Sulawesi itself.

Philippine relationships

It has been seen above that there are no grounds for deriving any but a small part of the Sulawesi mammal fauna from the Philippines: a few bats come from there, and Musser (1973) hints that a few rats may find their closest relatives there. A direct route between Sulawesi and the Philippines would have to pass via either the Talaud or Sangihe islands, so it is necessary to list the fauna of these two small groups.

The Talaud islands have 7 recorded species of mammals, the Sangihe islands 13 (Table 3). These figures reflect the distance of the two groups from Sulawesi; the Sangihe islands are within sight of the northern tip of the latter, the Talaud islands not so. All but two Sangihe species are known from Sulawesi, and all but two Talaud species — but this means twice as many proportionally. Apart from widespread, doubtless introduced species, only a single Talaud species, and no Sangihe species, inhabits the Philippines as well. An endemic species of bat is said to inhabit Talaud; Sangihe has no endemics at the species level.

Table 3

Mammals of Talaud and Sangihe Islands

			Other range
1. Talaud Islands			
MARSUPIALIA	Phalangeridae	*Phalanger ursinus* (Temminck, 1824)	Celebes
CHIROPTERA	Pteropodidae	*Pteropus hypomelanus* Temminck, 1853	Celebes, N. G.
		Acerodon humilis Andersen, 1909	Endemic
		Cynopterus brachyotis (Müller, 1838)	Celebes, Sundaland, Philippines
RODENTIA	Muridae	*Rattus rattus* (Linnaeus, 1758)	Widespread
		„*Rattus rattus talaudensis* Sody, 1941“ (?*argentiventer*)	Widespread
		Melomys fulgens Thomas, 1920	Seram
2. Sangihe Islands			
MARSUPIALIA	Phalangeridae	*Phalanger celebensis* (Gray, 1858)	Celebes, Halmahera
CHIROPTERA	Pteropodidae	*Rousettus celebensis* Andersen, 1907	Celebes
		Pteropus hypomelanus (Temminck, 1853)	Celebes, N. G.
		Pteropus caniceps (Gray, 1870)	Celebes, Halmahera
		Pteropus melanopogon Peters, 1867	Moluccas, N. G.
		Pteropus chrysoproctus Temminck, 1837	Seram
		Acerodon celebensis (Peters, 1867)	Celebes, Sula Is.
		Macroglossus lagochilus Matschie, 1899	Celebes, N. G.
CARNIVORA	Viverridae	*Paradoxurus hermaphroditus* (Pallas, 1777)	Widespread
RODENTIA	Sciuridae	*Callosciurus leucomus* (Forsten, 1844)	Celebes
	Muridae	*Rattus rattus* (Linnaeus, 1758)	Widespread
		Mus musculus Linnaeus, 1758	Widespread
PRIMATES	Tarsiidae	*Tarsius spectrum* (Pallas, 1779)	Celebes

It is of incidental interest to observe what sort of animals have crossed the "sweepstake route". Cuscus have made the journey to both island groups: but a different species in each case. It may not be irrelevant that the Sangihe *Phalanger celebensis sangirensis* is a typical member of its species, whereas the Talaud *P. ursinus melanotis* is not entirely typical of its species, showing some resemblances to *P. maculatus chrysorrhous* from Saleyer, Seram and the Bird's Head of Irian Jaya.

Melomys fulgens, a murid otherwise restricted to Seram, is the only other non-commensal, non-bat recorded from the Tabaud islands. In view of the resemblances of the Talaud cuscus to a Seram form, this takes on a considerable significance. The relationships of both species should be looked at again; it may be, for example that cuscus from both Sulawesi and Seram have reached Talaud and have formed a stable hybrid there.

Unlike Talaud, Sangihe has probably been populated almost entirely from Sulawesi. Here the surprises are the tarsier and a *Callosciurus*, especially the former which would not in theory be thought of as a resilient coloniser. Whatever conclusions one comes to, it is quite clear that the fauna of both island groups are depauperate — product of sweepstakes, not land bridges — and there is no trace of a major Philippine element such as would be expected were they intermediate staging posts in a southerly dispersal to Sulawesi.

Sundaland and Mainland relationships

Tarsius and *Babyrousa* are very ancient forms, finding their nearest relatives in the Oligocene of Europe. Their en route stopping-off points on their migrations to Sulawesi are unknown, nor the length of time they have been on the island. They are not unsuccessful, for *Babyrousa* has spread eastwards and survived competition from *Sus* — which the less archaic *Celebochoerus* has not — while *Tarsius* has established itself west of the Wallace Line.

Some of the other "old stratum" mammals of Sulawesi have links with the Middle Siwaliks (Dhok Pathan and especially Tatrot zones): certainly *Elephas celebensis*, *Celebochoerus* and *Anoa* do so, and possibly *Macaca* and *Stegodon*. In the case of *Anoa*, the Siwalik form is the most recent definite common ancestor of the Sulawesi subgenus and the nominate subgenus *Bubalus*.

Javanese fossil deposits are arranged in various zones, of which those earlier than Middle Pleistocene are Kabuh (with Trinil fauna), Pucangan (with Jetis fauna), Kali Glagah and Ci Julang. The last two are Pliocene or even earlier (they may or may not be chronologically separated), and according to Hehuwat et al. (1974) so are the bulk of the Pucangan beds. Von Koenigswald (1939) characterised the Ci Julang/Kali Glagah series as containing "Siva-Malayan fauna", while the later Jetis/Trinil fauna is said to be "Sino-Malayan". There are thus two levels. The Sino-Malayan fauna, with relationships in China, is by far the better known, while the earlier Siva-Malayan fauna is extremely poorly known.

It has been noted that some of the "old stratum" Sulawesi fauna appears to have Siwalik relationships, and clearly if these relationships are valid and the forms in question are a remnant Siva-Malayan fauna, then remains of their forbears should turn up in Ci Julang or Kali Glagah deposits in Java. Medway (1973) gives faunal lists of all the Javanese deposits, such as they are: no small mammals are known from the earlier deposits, and the larger mammals are on the whole poorly identified although it is probably significant to note with Medway, the absence of Siwalik grassland forms such as *Equus*. There is however a *Stegodon* tusk fragment in the Ci Julang beds, and *S. trigonocephalus* is recorded from Kali Glagah; *Elephas planifrons* occurs in both. Suids (*Sus stremmi* and *Sus brachygnathus*) are recorded from Kali Glagah — the former of uncertain affinities, the latter identified by Badoux (1959) on admittedly slender evidence with *Sus barbatus* (see above under *Sus verrucosus*). Several Bovids are found in these sediments, none of them really determinable (Hooijer 1958a). There are no primates or rodents, and no carnivores bar *Lutra* and some nondescript supposed Felids.

Some of these species apparently disappeared when the Sino-Malayan fauna entered Java. The most emphatic evidence is derived from elephants; the forebears of *E. maximus* entered Java with the Jetis fauna and at once replaced *E. planifrons* although a dwarf derivative of the latter seems to have lingered on for some time parallel to the dwarf Sulawesi elephant.

Geological history of Sulawesi

Audley-Charles et al. (1972) consider that Sulawesi is a composite island: its eastern and southeastern peninsulas are part of the Outer Banda Arc, which represents the margin of the Australian continent. The rotation of the latter, together with the western motion of New Guinea resulting from the movement of the Pacific plate, caused the realignment of the two arms of Sulawesi in a gamma-oriented, rather than a lambda-oriented position. The southern and northern peninsulas were part of Southeast Asia, and their junction with the other two arms is probably Pliocene in date: accompanied, as expected, by widespread orogeny.

It would not, however, be justified to assume that Sulawesi owes its Cuscuses to its eastern half; the cuscuses of the island, as discussed above, are simply not that distinct from those of New Guinea to allow such an early date of separation to be entertained, and it is not even certain whether any of eastern Sulawesi was above sea-level or that there was dry land between it and the Australian margin.

The history of Sulawesi as elucidated by plate tectonics has not altered the picture of its relations with Southeast Asia drawn by Van Bemmelen (1949), as far as the western half (southwestern and northern peninsulas) is concerned. The important part of this history for present purposes concerns the Pulau Laut Centre of Diastrophism. This would seem to be a large uplifted island, extending according to Van Bemmelen from the Mangkalihat peninsula southwards and across the Makassar Strait, curving around Pulau Laut to the southwest and ending near the Muriah volcano in Java. At the time of the existence of this island – Upper Pliocene according to Van Bemmelen – the present land areas of Southeastern Borneo and western Sulawesi were covered by sea, as was the northern part of East Java. It is in fact uncertain whether there was at any time a complete land bridge from Java or Borneo to Sulawesi; as the Ci Julang Faunal beds and other Pliocene sites in eastern Java are interbedded terrestrial and marine deposits it seems that there might from time to time have been a brief connection at least at the southern end between Java and the P. Laut Centre.

The submergence of the P. Laut Centre of Diastrophism is dated by Van Bemmelen to the onset of the Quarternary, and was accompanied by uplift of the surrounding areas. However the terms Quaternary, Pliocene and Pleistocene have only limited significance in this part of the world, as we have seen: the dating of *Homo modjokertensis* at Pucung to 1.9 ma puts this hominid, and the accompanying Jetis fauna, squarely into the Pliocene as most recently defined (Berggren and Van Couvering 1974), and most of the Pucangan Black Clays are Pliocene in age according to the newest estimate (Hehuwat et al. 1974). The corresponding level in India would be the upper part of the Tatrot zone (Middle Siwaliks): very neatly explaining the link between the Ci Julang/Kali Glagah faunas of Java and the Middle Siwaliks of India. To get the Siva-Malayan fauna into Sulawesi might require limited island-hopping or even no island-hopping at all, and to explain the absence of Sino-Malayan fauna in Sulawesi would mean the pushing back in time of the collapse of the P. Laut Centre to approximately Middle Pliocene – not impossible seeing the flexibility of such concepts as "Pliocene" in Southeast Asia.

Conclusions

The large mammalian fauna of Sulawesi nearly all belong to the "old faunal stratum", whose fossil aspect has been referred to by Hooijer (1958b) as the *Archidiskodon-Celebochoerus* fauna, a term that may require revision owing to the demise of the genus *Archidiskodon* (Maglio 1973). It has been shown that, wherever the relationships of the constituent species/genera can be traced, they are with forms from the Middle Siwaliks. A Siwalik-like fauna — the Siva-Malayan fauna of Von Koenigswald — has been found at two sites, Kali Glagah and Ci Julang, in Java, though this fauna is exceedingly poorly known. At some period in the late Tertiary a narrowing of seaways, possibly even a brief land-bridge, occurred between Java and Sulawesi in the shape of the Pulau Laut Centre of Diastrophism: this would have provided a relatively untraumatic mode of entry for large mammals, and its collapse at some time during the Pliocene widened the gaps considerably, keeping out the second faunal wave, the Sino-Malayan fauna.

Some of the small mammals of Sulawesi also probably derive from this early invasion, but lack of fossil remains of rodents and bats renders this hypothetical. Others of the rodent and bat fauna entered by chance crossing of seaways, almost entirely from the west; yet others, and some larger fauna, have been introduced by man in recent times. Proposed links with the Philippines do not stand up to critical examination; all mammalian faunal connections are amenable to explanations other than one of direct contact; and the faunas of Sangihe and Talaud, such as they are, show no evidence of any Philippine element, being derived from Sulawesi alone with (in the case of Talaud) a puzzling element with affinities with Seram.

At least one genus, *Tarsius*, may have evolved — from origins as yet unknown — on Sulawesi and spread to Sundaland and thence to the Philippines. It is here tentatively suggested, as a working hypothesis, that another genus to have evolved on Sulawesi and successfully invaded other lands might be *Rattus:* this genus is more diverse here than on other land masses of similar size, it has spread to Australasia as well as to Southeast Asia, it has specialised derivatives within Sulawesi *(Tateomys, Melasmothrix),* and it would apparently require fewer chance dispersals to get species out of Sulawesi than into it.

A number of hypotheses, some better grounded than others, have been put forward in this paper as explanations for the supposed realities of the faunal situation on Sulawesi as regards mammals. It is hoped that these may stimulate further thought on the matter, perhaps a little controversy, and above all, more research.

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Summary

Analysis of the mammalian fauna of Sulawesi suggests the existence of a basic "old stratum", deriving from a Pliocene invasion across the land-mass known as the Pulau Laut Centre of Diastrophism, of the Siva-Malayan fauna. Subsequently other elements entered Sulawesi by chance sea-crossing, almost entirely from Sundaland; there is no evidence of a significant contribution from the Philippines. Some mammals may have evolved in Sulawesi and later successfully colonised other areas.

Zusammenfassung

Die Herkunft der Säugetierfauna von Sulawesi (Celebes)

Die Analyse der Säugetierfauna von Sulawesi läßt auf die Existenz einer alten Basisschicht schließen. Diese stammt von einer pliozänen Einwanderung siva-malaiischer Faunenelemente ab, welche über die Landmassen des „Pulau Laut Centre of Diastrophism" erfolgte. Später erreichten andere Elemente Sulawesi und zwar durch zufällige Meeresüberquerungen, jedoch immer nur von den großen Sundainseln ausgehend. Für eine Mitwirkung philippinischer Faunenelemente ist kein signifikanter Hinweis zu erbringen. Einige Säugetierarten haben sich möglicherweise auf Sulawesi entwickelt und später andere Gebiete erfolgreich besiedelt.

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Morphometrische Untersuchungen an algerischen Wimperspitzmäusen

2. Die *Crocidura suaveolens*-Gruppe (Mammalia: Insectivora)

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Direktor: Prof. Dr. W. Schäfer

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Nachdem in der ersten Untersuchung über algerische Wimperspitzmäuse die *Crocidura russula*-Gruppe abgehandelt wurde (Vesmanis 1975), soll in der nachfolgenden Darstellung die *Crocidura suaveolens*-Gruppe vorgestellt und diskutiert werden.

Abkürzungen

a. Schädelmaße: CIL = Condyloincisiv-Länge; CBL = Condylobasal-Länge; PL = Prosthion — Lambda; SKB = Schädelkapsel-Breite; SB = Staphylion — Basion; SV = Spenobasion — Vertex; MSQ = Maxillofrontale — Squamosum; IB = Interorbital-Breite; JB = Joch-Breite; LB = Lacrymale Breite; GL = Gaumen-Länge; RB = Rostrale Breite; RL = Rostrum-Länge, gemessen zwischen I-Alveole und P^4-Alveole; AI = Angulare — incl. Incisivus; UKL = Unterkiefer-Länge; CL = Condylar-Länge; CH = Coronar-Höhe; CB = Coronar-Breite; PCH = Postcoronar-Höhe; GKL = Gelenkkopf-Länge; GKB = Gelenkkopf-Breite.

b. Zahnmaße: M-M = maximale Breite über den Molaren (Kronen); OZL = obere Zahnreihen-Länge, I-M^3; P^4-M^3 = Zahnreihen-Länge, P^4-M^3; LP^4 = Länge, P^4, Vorder-

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